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Potamodromous brown trout movements in the North of the Iberian Peninsula: Modelling past, present and future based on continuous fishway monitoring

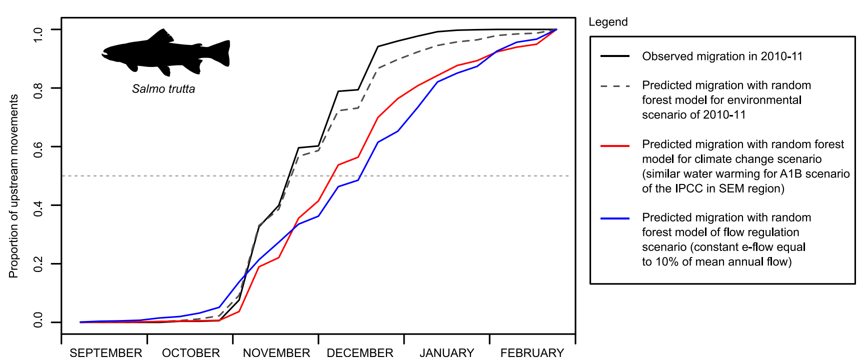
Ana García-Vega [a,]*, Francisco Javier Sanz-Ronda [a], Leandro Fernandes Celestino [b], Sergio Makrakis [b], Pedro M. Leunda [c]

[a] Department of Hydraulics and Hydrology, University of Valladolid, Avenida de Madrid 44, Campus La Yutera, 34004 Palencia, Spain
[b] Grupo de Pesquisa em Tecnologia em Ecohidráulica e Conservação de Recursos Pesqueiros e Hídricos – GETECH, Universidade Estadual do Oeste do Paraná, Jardim Santa Maria, Toledo, Brazil
[c] Gestión Ambiental de Navarra, S.A. Calle Padre Adoain, 219 bajo, 31015 Pamplona/Iruña, Spain

HIGHLIGHTS

- Anthropogenic impacts on hydrology, climate and habitat threaten freshwater fish.
- Long-term study of potamodromous brown trout in its southern distribution area
- Continuous fishway monitoring showed captures throughout the year.
- Random forest model predicted accurately timing and quantification of migration.
- Climate change and flow regulation scenarios would delay spawning migration.

GRAPHICAL ABSTRACT



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ABSTRACT

Brown trout uses river flow and thermal regimens as main stimuli for initiating and maintaining behavioral reactions such as migration and spawning. Therefore, anthropogenic alterations on these factors may have strong impacts on its populations. The aim of this work is to understand these consequences by assessing potamodromous brown trout movements in the past and present, and to model future responses. For this, brown trout movements in a fishway in the Marin River (Bidasoa basin, Northern Iberian Peninsula) have been monitored from 2008 to 2017. Random forest regression has been used to assess the influence of environmental variables on brown trout movements and to model the response under hypothetical climatic and hydrological scenarios. Results show that brown trout uses the fishway during the whole year, with more upstream movements during the spawning season. The model is able to predict accurately the timing and number of migrants. Its use under hypothetical climate change and flow regulation scenarios shows a delay in the migration time. Therefore, modelling using large time series can be a powerful tool to define management and conservation strategies and prepare compensation measures for future scenarios.

* Corresponding author.
E-mail addresses: ana.garcia.vega@iaf.uva.es, (A. García-Vega), jsanz@iaf.uva.es, (F.J. Sanz-Ronda), le_celestino@hotmail.com, (L. Fernandes Celestino), sergio.makrakis@unioeste.br, (S. Makrakis), pleundau@gan-nik.es (P.M. Leunda).

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1. Introduction

Freshwater environments are subject to multiple stressors derived from the use that the human society makes of rivers (e.g. irrigation, power generation, flow control or industrial and domestic supply), which can alter ecological patterns and processes (Branco et al., 2016; Segurado et al., 2016). Among these stressors, river fragmentation and alterations on natural river flow and thermal regimens are the most important affecting freshwater ecosystems (Feng et al., 2018; Jones and Petreman, 2015; Nilsson et al., 2005). Near future scenarios suggest an aggravation of this situation, with an increase of the magnitude and number of stressors acting upon river ecosystems and an increase of the possible interactions (Segurado et al., 2016). In one hand, climatic change shows potential alterations in water temperature and in the magnitude, intensity and frequency of rainfall and consequently in river flow (Solomon et al., 2007). In the other hand, human population growth can cause water scarcity due to the increase in water demand and water pollution as result of industrial, domestic and agricultural waste water (Almodóvar et al., 2012; Branco et al., 2016; Segurado et al., 2016; Vörösmarty et al., 2000). Understanding the isolated and combined impact of all these alterations is necessary for the prediction of responses to changing environments and for the establishment of impact mitigation and compensation measures (Segurado et al., 2016).

Fish are one of the most sensible aquatic organisms to these stressors (Clavero et al., 2004). Freshwater fish use flow and thermal regimens as ecological timers for initiating and maintaining behavioral reactions such migration, feeding and spawning (Lucas et al., 2001). More specifically, water temperature has effects on the developmental rate, growth, sexual maturation and food consumption across life-stages whereas water flow influences shelter, feeding, migration and spawning opportunities (Jonsson and Jonsson, 2011). Alterations on these factors can lead in a shift on the phenology and a consequent mismatch between available and necessary resources (Otero et al., 2014), endangering the persistence of many migratory fish species (Shuter et al., 2012), such as the brown trout (*Salmo trutta*, Linnaeus 1758).

Brown trout performs multiple movements along its life cycle, from small-scale migrations, such as alevin post-emergence dispersion from spawning ground over the nearby streambed, to longer ones in order to find feeding, refuge or spawning habitats (Aarestrup et al., 2018; Lucas et al., 2001). This species can display diverse life history tactics, from anadromy (sea trout) to potamodromy (riverine trout), or even partial migrations, with both short (resident trout) and long-distance movements (migratory trout) (Jonsson and Jonsson, 1993). This ecological plasticity gives them the ability to survive and adapt, up to some extent, to potential perturbations over time (e.g. population imbalances, river fragmentation or climatic alterations) (Aarestrup et al., 2018).

Brown trout is a world-wide distributed species. Its natural distribution spreads over Europe, North Africa and West Asia, but also it has been introduced in South Africa, Russia, North and South America among others (Klemetsen et al., 2003). Its migration patterns and cues are affected by latitude, with a local variation dependence on environmental conditions (Aarestrup et al., 2018). In general, most important upstream movements of southern populations occur in autumn and winter (Doadrio, 2002; García-Vega et al., 2017). These movements are related to the search of adequate spawning sites (García de Jalón, 1992) and are usually triggered by changes in photoperiod and water temperature (due to its influence on biological functions (Jonsson and Jonsson, 2011; Thorpe, 1989)) and are favoured by high flows (e.g. overcoming obstacles, predator avoidance (Ovidio and Philippart, 2002; Svendsen et al., 2004)). In addition, thermoregulatory movements outside of the reproductive season have been reported (García-Vega et al., 2017; Ovidio, 1999).

Brown trout has been deeply studied due to its economic and historical importance (Northcote and Lobón-Cerviá, 2008). However, most of available research on brown trout migration has been focused on anadromous populations, mainly during reproductive season or limited time period, and studies in the south of its natural distribution range are still scarce (Benitez et al., 2015; Thurow, 2016). Here, we present a long-term and full-year study (from 2008 to 2017) of potamodromous brown trout (hereafter referred to as trout) migration in a small-size river in the Northern Iberian Peninsula. The main aim of this work is to assess and model trout movements in the past, present and future, using a holistic approach, encompassing biological, climatic and hydrological variables. The specific objectives to achieve this are to: (1) identify periods with most upstream movements and the possible variations among years; (2) evaluate the relation of these movements with biological and environmental variables; (3) develop a model able to predict when upstream movements are more likely to occur; and (4) evaluate the consequences of climate change and flow regulation scenarios in the migration timing.

Unravelling the movement patterns of potamodromous species is therefore important to enhance conservation efforts, overall taking into account the future projections on water demand and climate change. Models based on long time series and environmental and climatic variables can have direct application in the management and conservation strategies. Particularly in climate change and flow regulation scenarios these models can be an essential tool to stablish mitigation measures (e.g. environmental flows, fishways), adequate scheduling of river restoration activities and fisheries stock management.

2. Materials and methods

2.1. Study area

The study was carried out in the Marin River, a small-size river, tributary of the Bidasoa River (Navarre, Spain). The study reach is located in Oronoz-Mugairi village (ED50 43°8′N, 1°36.5′W) (Fig. 1), with an altitude of 160 m above mean sea level. It is placed in the *trout zone* (Huet, 1954), specifically in the *Epirhithron zone* (Illies and Botoseanu, 1963), and belongs to the A3 category (cobble bed river, low sinuosity and a slope of 0.04–0.099 m m^{-1}) (Rosgen and Silvey, 1996). The mean annual discharge is 2.08 m^3 s^{-1} and the mean annual water temperature of 11.6 °C. According to physical and chemical analysis (mean values of $PO_4 = 0.03$ mg L^{-1}, $NH_4 = 0.03$ mg L^{-1}, $NO_3 = 5.29$ mg L^{-1}, $O_2 = 9{,}77$ mg L^{-1}, pH = 8.08; Government of Navarre, 2015), the water quality is *very good* (based on Spanish law RD 817/2015). The main species in this river reach is the potamodromous brown trout, although Atlantic salmon *Salmo salar*, Linnaeus 1758 and European eel *Anguilla anguilla* (Linnaeus 1758) also occur in very low densities. The distance from the sea (51.4 km) and the presence of at least 10 transversal obstacles in the Bidasoa River, downstream of Mugairi fishway (weirs and dams, not all of them were equipped with a fishway, as far as the end of the study date) restricts the presence of anadromous trout in this tributary (Gosset et al., 2006).

To obtain information about trout movements, a continuous monitoring of a fishway was carried out. Fishways, in addition to facilitate the free movement of fish through cross-sectional obstacles in rivers, can be used as structures to study upstream fish movements, as they act as corridors of mandatory passage (Travade and Larinier, 2002). The Mugairi fishway was built in 1994 in a derivation weir of a salmonid fish farm that belongs to the Government of Navarre (Fig. 1). It is a gravity weir of 4.5 m high and 24 m wide. The fishway is a pool and weir type with 14 pools. Pools have an average width and length of 1.3 m and 2.1 m respectively, with a slope of 11%. Each cross-wall has a submerged notch of 0.2 m of mean width and 0.65 m of mean sill height and a squared bottom orifice of 0.17 m mean side length. The fishway design flow was 0.15 m^3 s^{-1}, with a mean water depth of 0.9 m, water drop of 0.25 m and volumetric power dissipation of 140 W m^{-3} during design discharge (Fuentes-Pérez et al., 2017). The geometric and hydraulic parameters inside the fishway are in the range of fishway design recommendations (FAO/DVWK, 2002; Larinier, 2002).

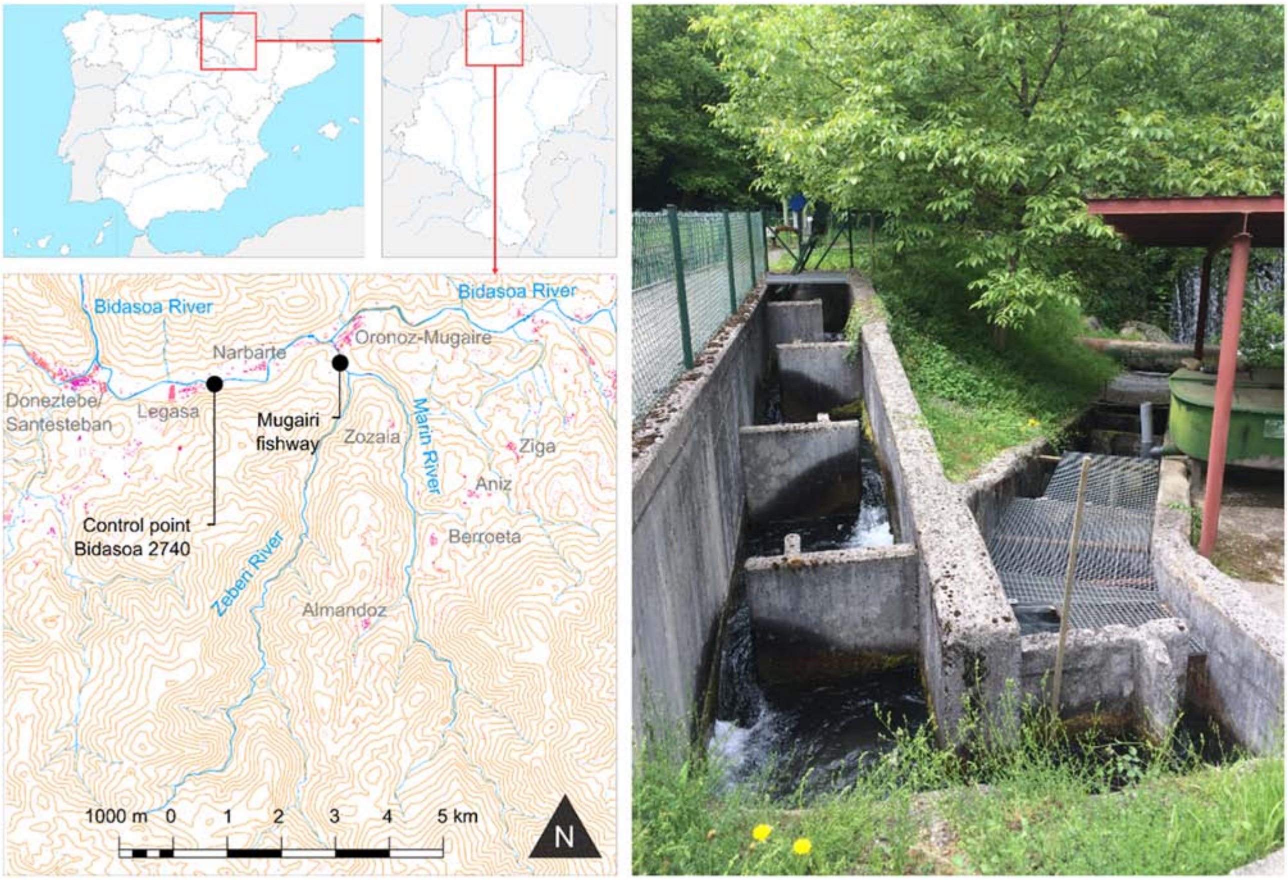

Fig. 1. Location of the Mugairi fishway in the Marin River (Oronoz-Mugairi, Navarre), in the north of the Iberian Peninsula, and picture of the fishway.

2.2. Sampling procedure

The fishway was monitored by the fish farm staff from 01/09/2008 to 17/03/2017 two-three times a week during the whole year, increasing the monitoring frequency to once a day when high migration rates occurred. Study years were considered starting on 1st September (when spawning movements were more likely to start) and ending on 31st August, and were named with the number of the both integral year (e.g. the study year 2008–09 goes from 01/09/2008 to 31/08/2009).

For sampling, the fishway was closed by means of portable gates in the most downstream cross-wall of the fishway and in the turning pool. The gate of the fishway is equipped with a fish net that prevents fish from exiting the fishway in the upstream direction. Fish were captured with a fish net within the fishway and then transferred to a 1000 L tank with continuous water supply provided by a water pump. Visual identification of the species was carried out. The captured trout were measured (fork length, FL, in mm) and sex identified based on secondary external sexual characters. Mature brown trout usually exhibit sexual dimorphism which allows sex differentiation (male and female), whereas immature individuals are monomorphic, which hinders the sex differentiation (sex unidentified) (Reyes-Gavilán et al., 1997). Finally, trout were released upstream of the weir to continue their migration.

2.3. Environmental variables

Photoperiod, water temperature and river flow were selected as environmental variables that could trigger or be related to the trout migration (García-Vega et al., 2017; Jonsson and Jonsson, 2011). Photoperiod (P, in h) corresponded with the daylength (time between sunrise and sunset) and was calculated with the Brock model (Brock, 1981). Water temperature (T, in °C) was monitored (HOBO Data Logger U14-002, Onset ©) by the Government of Navarre throughout the day at 6 h intervals (water temperature previous to the equipment installation (06/02/2009) and missing values due to technical problems (from 09/10/2013 to 30/01/2014) were completed with a linear regression ($R^2 = 0.8905$) with air temperature (Bertiz weather station, daily frequency) as dependent variable (Webb et al., 2003)). Due to the absence of gauging stations in the Marin River, flow data (Q, in $m^3\ s^{-1}$) were obtained by river basin comparison (Martínez de Azagra and Navarro, 1996) from its main tributary, the Zeberi River (AN943 Oronoz-Mugariri gauging station, daily frequency, Government of Navarre, 2016) (Fig. 1).

2.4. Data analysis and modelling

2.4.1. Captured fish characteristics

Frequency analysis of the number of captures by size and sex categories (male, female and unidentified sex) was performed. Binomial test was performed to find differences between number of captures by sex and test for equality of proportions was performed to find differences among years. In addition, Mann-Whitney Wilcoxon (MW) test was used to find differences in FL by sex and Kruskall-Wallis (KW) test was performed to find differences in FL among years. These non-parametric tests were applied as variables were not normally distributed. When KW test was significant, post hoc Dunn's Multiple Comparison Test with Bonferroni correction was performed. In order to identify life stages, distinction between adult or juvenile trout was made. Trout sexual maturation in Iberian rivers is achieved between 2+ and 3+ ages (Doadrio, 2002), which coincides approximately with 20 cm FL in the Bidasoa basin (Laplanche et al., in prep.). This FL is also the minimum catch size described in the Navarre fishing law (Government of Navarre, 2018). Therefore, 20 cm FL was established as cut-off for adult size.

2.4.2. Captures throughout time

Frequency analysis of the number of captures by month and year were performed. In addition, linear regression between number of captures in the fishway (during the period autumn-winter, i.e. from September to February) and the population density estimates from the Bidasoa River (during the previous August) next to the confluence with the Marin River was carried out to find a relation between the captures in the fishway and the population in the river. Trout population estimates where gathered by the Fishing Service of the Government of Navarre from annual electrofishing surveys (captures of adult and juvenile trout during August) in a control point (ref. Bidasoa 2740) next to Legasa village (Fig. 1).

To check differences in number of captures among months and years, KW and Dunn tests were performed. Moreover, to detect whether pattern of movements varies among years and sexes (no distinction by life stage was considered because the low number of captured juveniles), survival analysis techniques were used, by applying the concept of survival time (time until an event occurs) to migration time (time until a fish is captured in the fishway). This approach was selected because is a powerful statistical analysis to assess differences among categorical independent variables (sex or years) when the dependent variable is time or some function time-dependent (Lee and Wang, 2003). For this Kaplan-Meier (KM) survival curves (Kaplan and Meier, 1958) were determined to show different patterns by sex and to determine the median migration date (the week when the 50% of the captures in the fishway has occurred), for the whole year as well as for the two periods autumn–winter and spring–summer. As the revision periodicity of the fishways varied over time, captures were grouped (summed) by week for the analysis, considering the starting point the first week of September. Log Rank test was used for KM curve comparison (Mantel, 1966). For survival analysis we used the *survival* package (Therneau and Grambsch, 2000) of the *R* software (release 3.2.3, R Core Team, 2016). In addition, linear regression between mean weekly FL and time (in weeks) was carried out in order to identify different movement pattern by size throughout the year. Mean FL by week was used as dependent variable in order to get a representative value because the number of captures was different each week.

2.4.3. Environmental variables

Comparisons of the environmental variables among years were performed using KW and Dunn tests. The relation among the environmental variables (mean weekly P, T and Q and their variations with respect to the previous week (actual minus previous) ΔT and ΔQ) was analyzed by means of Spearman correlations.

2.4.4. Modelling past and present scenarios

The influence of the environmental variables on the number of captures was modelled by means of Random Forest (RF) regression. RF has been widely applied in ecology (Breiman, 2001; Cutler et al., 2007) and more recently in freshwater fish studies (Markovic et al., 2012; Vezza et al., 2015), showing good performance in fish abundance prediction and response to environmental alterations (Ward et al., 2014). RF is a statistical ensemble method based on the combination of a multitude of decision trees which are used to determine the mean prediction of the individual trees (Breiman, 2001). For the RF regression, number of weekly captures was considered as dependent variable while the environmental variables (T, ΔT, Q, ΔQ and P) were the independent ones. Due to the low number of captures during the period spring–summer (from March to August), RF regression was only applied for the data of the period autumn–winter (from September to February). Besides quantifying the migration (weekly number of captures), in order to check if the model was able to predict the migration timing (weeks with more number of captures), the predicted values were transformed into proportions for comparison with the observed ones.

We used the *randomForest* (Liaw and Wiener, 2002) *R* package, in which the number of trees to grow was set at 500 while the number of variables randomly sampled as candidates at each split was set at the square root of the number of input variables (recommended default settings). In RF, there is no need for a separate test set for cross-validation as it is performed internally during the run (Breiman, 2001), so RF model was built without data splitting to fully extract the ecological information from the observed data. However, validation of the model was evaluated by the coefficient of determination (R^2) for both, the number of captures (migration quantification) and the proportion of captures by week (migration timing). Because in RF extreme observations are estimated using averages of response values that are closer to those observations, large values of the regression function may be underestimated and small values of the regression function may be overestimated (Zhang and Lu, 2012). This issue was resolved by applying a linear bias correction. The importance of the environmental variables was measured using the increase in mean squared error (MSE) of predictions, which

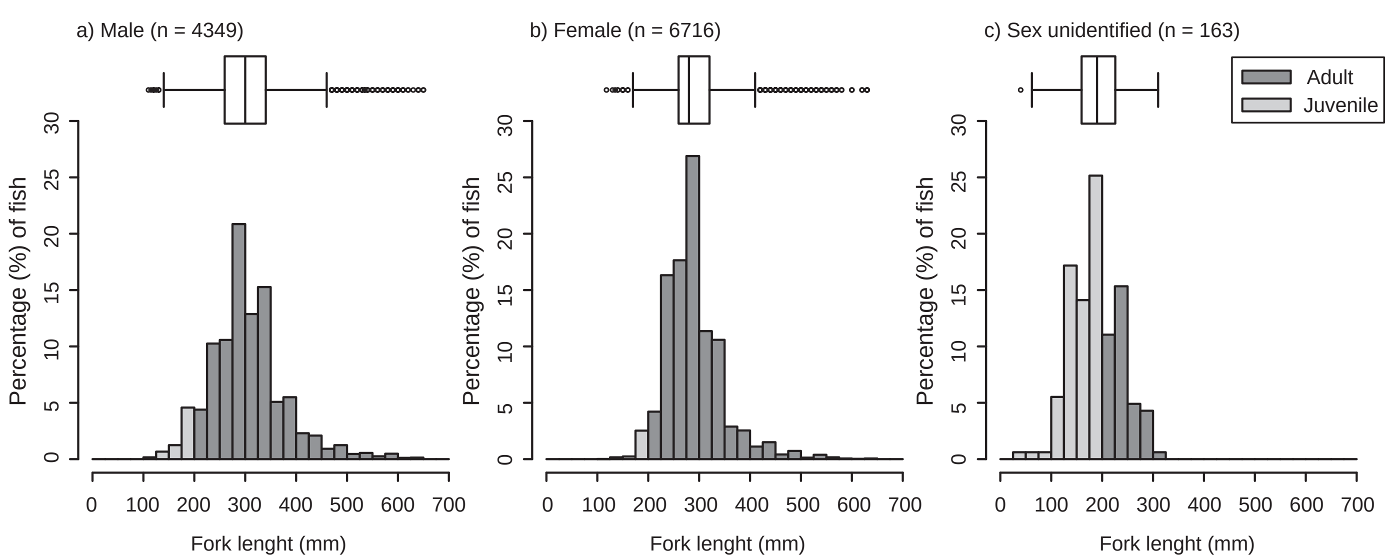

Fig. 2. Boxplot and histogram of the size distribution of the all captured trout by sex and life stage.

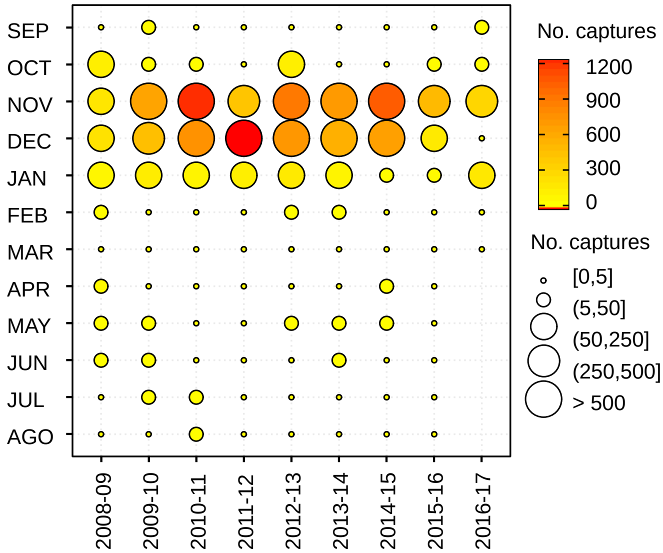

Fig. 3. Heatmap of the number of captures along time. Detailed information about number of captures by month and year, as well as mean values, can be found in Appendix A.

represents how much the model fit decreases when a variable drops of the model (the higher number, the more important). Partial dependence plots for environmental variables were obtained from RF in order to characterize the marginal effect of a variable in the model.

2.4.5. Modelling hypothetical future scenarios

In order to evaluate the influence of climate change and a possible increase in water demand, three hypothetical future scenarios were evaluated with the developed RF model. The scenario 1 represents a climate change scenario with a water temperature increase similar to the increase of air temperature in the A1B scenario of the Intergovernmental Panel on Climate Change (IPCC) for the Southern Europe and Mediterranean (SEM) region: +3.3 °C in autumn (September–November) and +2.6 °C in winter (December–February) (Solomon et al., 2007), and rest of variables equal to the observed ones. A1B scenario was chosen because, despite the IPCC did not state that any of the climate change scenarios of the report were more likely to occur than others, they used it as baseline scenario for the future regional projections. The scenario 2 represents a river water regulation, with a poor environmental flow, in order to recreate an intensive river regulation, based on the Tennant method: constant flow of 10% of the mean annual flow, that provides the minimum protection of the physical habitat for aquatic fauna (Tennant, 1976), i.e. $Q = 0.208\ m^3\ s^{-1}$, but without considering seasonality, i.e. $\Delta Q = 0$, and rest of variables equal to the observed ones. Finally, the scenario 3 is a combination of the scenarios 1 and 2. Due to significant differences on median migration dates and environmental variables among years, the nine studied years were used as base for nine future projections instead only one projection of an averaged scenario.

3. Results

3.1. Captured fish characteristics

In the whole study period, 11,228 trout were captured in the fishway, where 39% were male, 60% were female and 1% were sex unidentified (Table A.1). Individuals were mainly presented in adult stage (96%). Global sex rate was 1.5 female for each male (test for equality of proportions: $\chi^2 = 57.525$; p-value < 0.0001), with the number of females significantly greater than the number of males in all years, in exception of 2015–16, where both proportions were similar (p-value = 0.1163) (Table A.1).

FL was in the range 40–650 mm, with an average of 297 ± 66 mm and a median of 290 mm. Results of KW test showed that there were significant differences in FL among years ($\chi^2 = 291.28$; p-value < 0.0001), with significantly shorter FL on 2014–15 and longer on 2011–12 and 2013–14 (Tables A.1 and A.2). Males were significantly larger than females (except for the years 2009–10 and 2013–14 when there was no difference), and the unidentified sex trout were smaller than the identified ones (Table A.1 and Fig. 2).

3.2. Captures throughout time

Number of captures in the fishway varied among months (Fig. 3 and Table A.3). In general, November and December were the months with

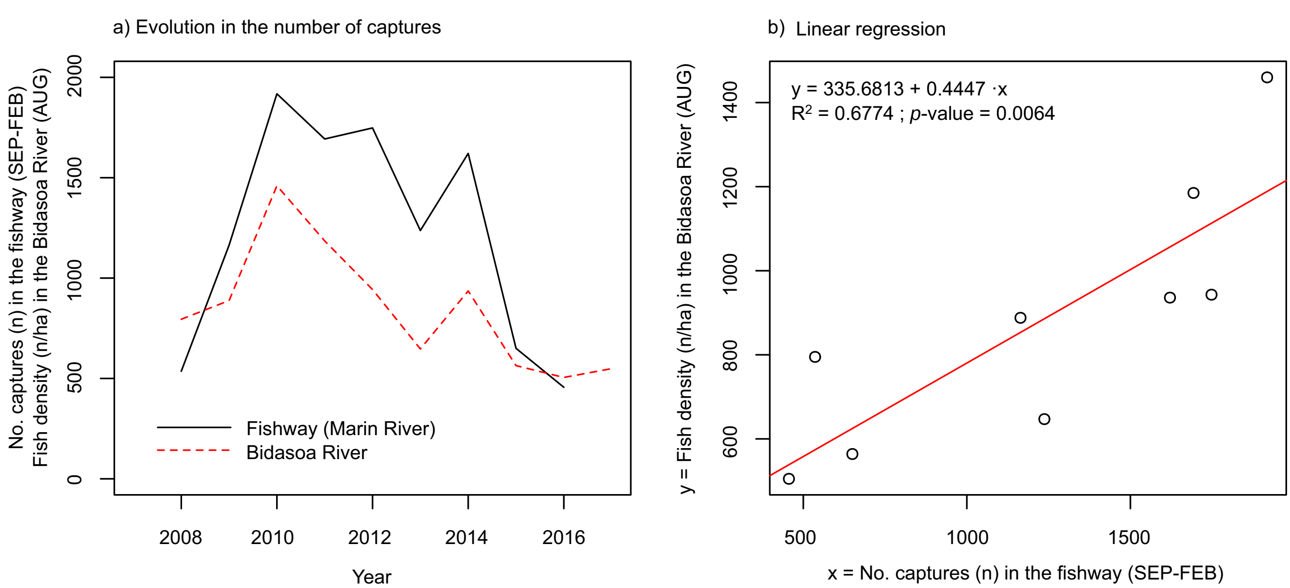

Fig. 4. Comparison between the number of captures in the fishway (Marin River) from September to February and the electrofishing captured trout in the Bidasoa River in August. a) Evolution in the number of captures. b) Linear regression between the number of fish captured in the fishway (Marin River) in September–February (x) and the fish density captured in the Bidasoa River in August (y).

the highest number of captures (88% of captures). Results of KW test showed that there were significant differences in number of captures among months ($\chi^2 = 69.193$; p-value < 0.0001), with November, December and January significantly different to the most part of the remaining months (Table A.4). On the other hand, there were not significant differences on number of captures among years ($\chi^2 = 8$; p-value = 0.4335). Linear regression showed a positive relation between the number of captures in the Bidasoa River in summer with the captures in the fishway the following autumn–winter (Fig. 4).

Migration patterns were quite similar in all years (Fig. 5, black solid lines), with more number of captures in November and December. Nevertheless, Log Rank test showed that the global migration curves were significantly different by year ($\chi^2 = 389$, p-value < 0.0001) and in 2011–12 the median migration date was considerably longer than other years, whereas in 2009–10, 2010–11 and 2016–17 was shorter (Table 1).

In the years 2008–09, 2015–16 and 2016–17, years that corresponded with the lowest number of captures, KM curves of

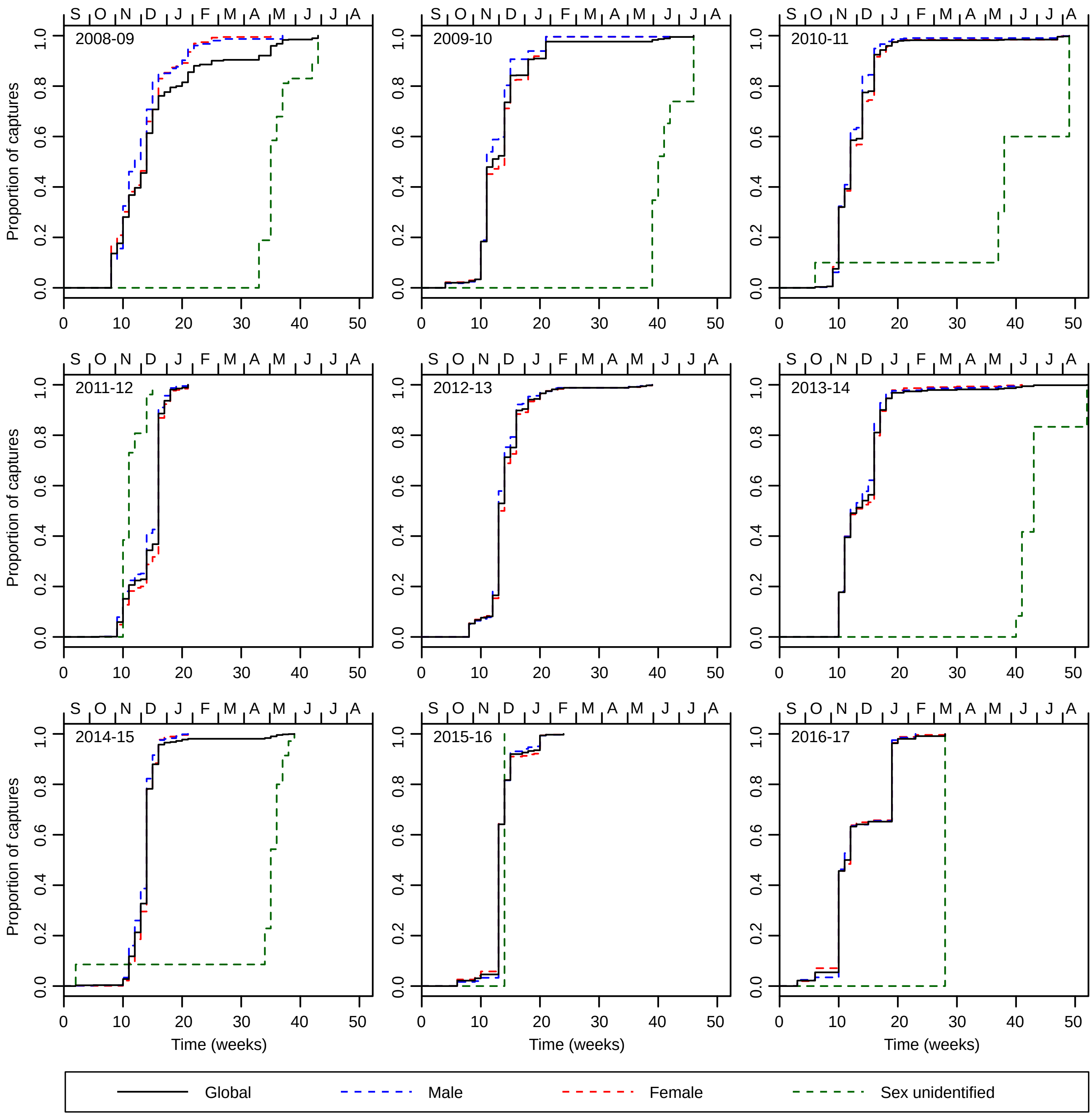

Fig. 5. Kaplan-Meier survival curves by sex category (representation of 1 − S(t) where S(t) is the survival function). Number of fish for each category, year and month are in Tables A.1 and A.3.

Table 1
Comparisons of median migration date (week when the 50% of the captures in the fishway has occurred, starting from September) by year. Results of Log Rank test for Kaplan-Meier curve (Fig. 5) comparison are shown (*p* stands for *p*-value).

	2008-09	2009-10	2010-11	2011-12	2012-13	2013-14	2014-15	2015-16	2016-17	Total
All captures whole period (SEP-AUG)	14	12	12	16	13	13	14	13	11.5	14
median migration date	(n = 595)	(n = 1192)	(n = 1953)	(n = 1693)	(n = 1769)	(n = 1263)	(n = 1653)	(n = 650)	(n = 460)	(n = 11229)
All captures spring-summer (MAR-AUG)	35	41	47	-	37	40	35.5	-	28	38
median migration date	(n = 59)	(n = 28)	(n = 35)	(n = 0)	(n = 21)	(n = 26)	(n = 32)	(n = 0)	(n = 4)	(n = 205)
All captures autumn-winter (SEP-FEB)	13	12	12	16	13	12	14	13	11	14
median migration date	(n = 536)	(n = 1164)	(n = 1918)	(n = 1693)	(n = 1748)	(n = 1237)	(n = 1621)	(n = 650)	(n = 456)	(n = 11024)
Male autumn-winter (SEP-FEB)	12	11	12	16	13	12	14	13	11	13
median migration date	(n = 151)	(n = 491)	(n = 741)	(n = 624)	(n = 659)	(n = 495)	(n = 654)	(n = 304)	(n = 203)	(n = 4322)
Female autumn-winter (SEP-FEB)	14	14	12	16	13	13	14	13	12	14
median migration date	(n = 385)	(n = 673)	(n = 1176)	(n = 1043)	(n = 1089)	(n = 742)	(n = 964)	(n = 345)	(n = 253)	(n = 6671)
Log Rank test (KM curve comparison)	$\chi^2 = 2.6$	$\chi^2 = 12.6$	$\chi^2 = 13.0$	$\chi^2 = 24.0$	$\chi^2 = 12.8$	$\chi^2 = 7.7$	$\chi^2 = 12.5$	$\chi^2 = 0.1$	$\chi^2 = 0$	$\chi^2 = 66.3$
male vs female autumn-winter (SEP-FEB)	$p = 0.107$	$p = 0.0004$	$p = 0.0003$	$p < 0.0001$	$p = 0.0003$	$p = 0.0055$	$p = 0.0004$	$p = 0.8060$	$p = 0.8570$	$p < 0.0001$

females and males were found no significantly different (Fig. 5, red and blue dashed lines respectively, and Table 1). However, in the remaining years, although the patterns of both curves were quite similar, they were significantly different, with males captured slightly earlier than females and being the curves for the latter slightly more staggered. In the other hand, sex unidentified trout (Fig. 5, green dashed lines, and Table 1) were captured in all years significantly later than identified ones, except for 2011–12 that they were captured significantly before and in 2015–16 that there were no differences (there was only one sex unidentified trout). Moreover, mean FL significantly decreased with the time, i.e., trout with longer FL (in general and for both sexes) moved, in general, earlier than the shorter ones (Fig. 6).

3.3. Environmental variables

There were not significant differences in the environmental variables among years except for the flow (Table A.5), as 2010–11 was the year with the lowest mean annual flow (1.208 $m^3\ s^{-1}$) with very low values during autumn–winter as well as in spring–summer, and in the other hand, 2012–13 was the year with the highest spring flows (Fig. 7).

Table 2 shows the range of the environmental variables during the study period as well as the range of each variable within trout movements occurred. For the period autumn–winter, all variables were significantly correlated among them (Table 2), in exception of their variation, with only Q and ΔQ significantly correlated.

3.4. Modelling past and present scenarios

RF regression model showed a good performance in the prediction of number of captures ($R^2 = 0.84$, MSE = 2041.77), improving the model to a great extent after the linear bias correction ($R^2 = 0.91$, MSE = 1250.05; Fig. 8). In addition, RF model was able to predict accurately the migration timing (Fig. 9).

The most important variable for predicting the number of captures was the water temperature followed by the flow variation respect to the previous week and the river flow, then the photoperiod and in last

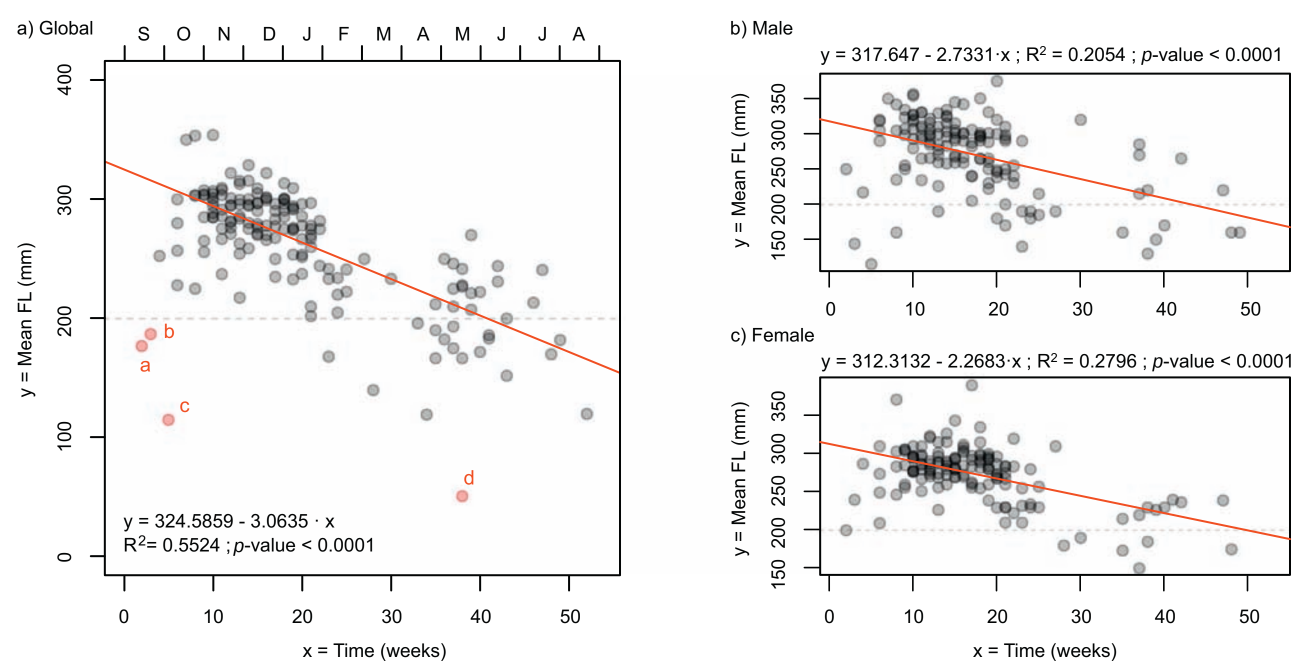

Fig. 6. Scatterplot of the mean FL (y) against time in weeks (x) considering, for a) all captures (where, four outliers (caused by few fish caught) were excluded in the analysis: point a (week 2 of 2014–15, n = 5), b (week 3 of 2016–17, n = 10), c (week 5 of 2014–15, n = 1) and d (week 38 of 2014–15, n = 2)), b) male and c) female captured trout. Red solid lines represent the regression lines whereas the gray dashed lines are the limit of the size between adults and juveniles.

place the water temperature variation with respect to the previous week (Figs. 7 and 10a). According to the partial dependence plots, the range 10 °C–12 °C of water temperature was associated with more captures (Fig. 10b), without a clear pattern in its variation with respect the previous week (Fig. 10c). In addition, low values of photoperiod (<10 h) showed a high influence on the number of captures (Fig. 10d). Finally, high values of mean weekly flows (Fig. 10e) and positive differences with respect to the previous week (i.e. flow increase) (Fig. 10f) were related to more number of captures, especially in the range from 2 to 4 $m^3 s^{-1}$.

3.5. Modelling hypothetical future scenarios

Simulated patterns of captures were different for the three hypothetical considered scenarios (Fig. 11). For scenario 1, the captures along time were delayed with respect to the observed in past scenarios (mean delay in median migration date of 4 ± 2 weeks) and more number of captures were expected, whereas scenario 2 and scenario 3 showed a continuous pattern of migration with lower number of captures and with also a delayed median migration date (3 ± 1 weeks and 4 ± 1 weeks respectively) respect to the observed in past scenarios (Fig. 11).

4. Discussion

This study analyzes and models, through a long-term and full-year monitoring and with a holistic approach, the upstream migration of potamodromous brown trout over nine years in a river system of the Iberian Peninsula and shows its application to estimate future migration responses to possible climatic change and flow regulation scenarios.

To achieve this, fish captures in a fishway were used. Upstream migration occurred through the fishway. However, due to the

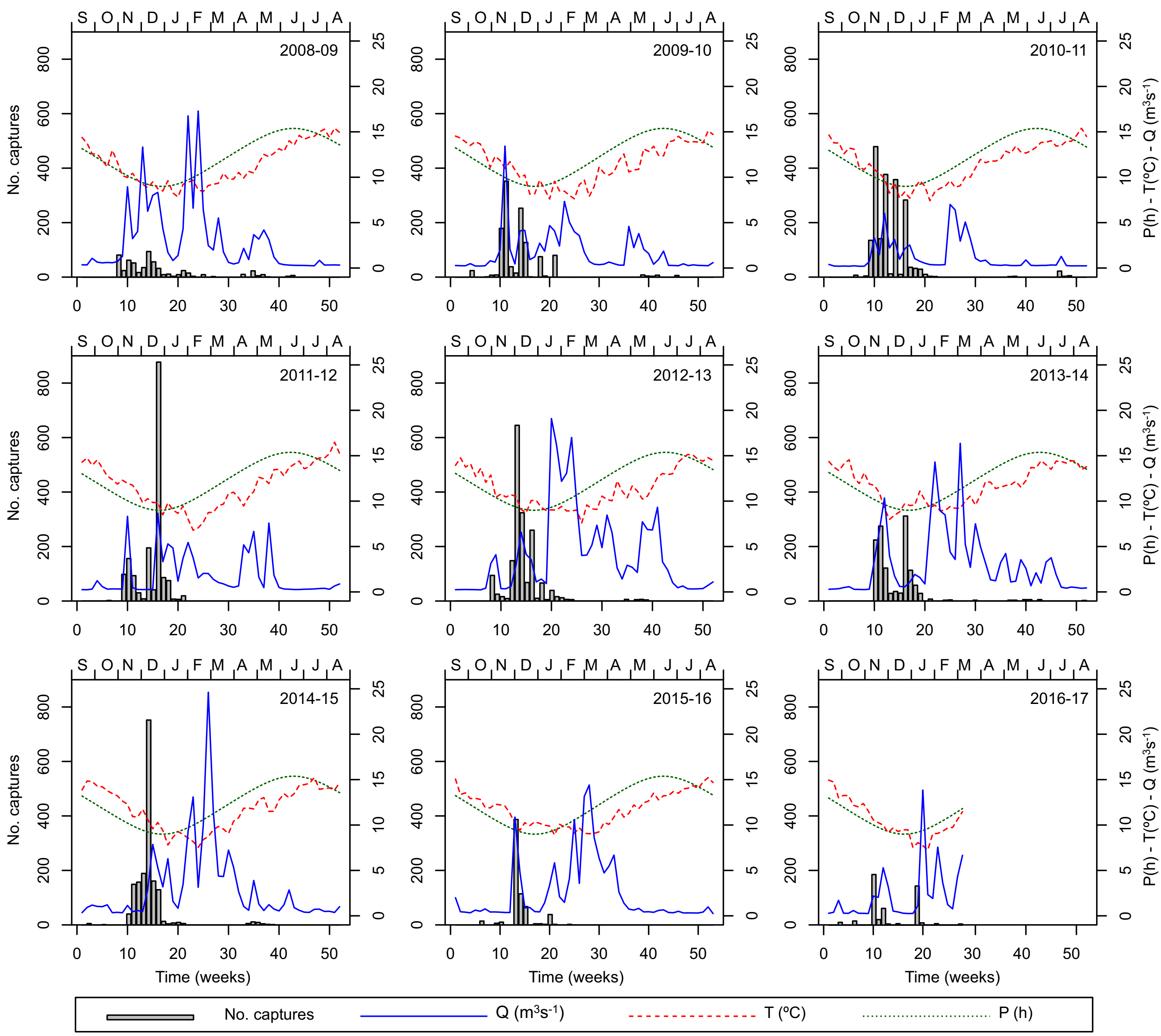

Fig. 7. Mean weekly river flow (Q, in $m^3 s^{-1}$), water temperature (T, in °C), photoperiod (P, in h) and number of captures by year for the study period (detailed information of number of captures by month and year can be found in Table A.3).

Table 2
Description of the environmental variables. a) Range of variation of the environmental variables (variable range) and range of each variable within trout movements occurred (movement range). b) Spearman correlation test (correlation coefficients (ρ) and p-values). Values above the diagonal correspond to the period March–August and below the diagonal to the period September–February.

a) Range of environmental variables and trout movements

	Water temperature (°C)		River flow ($m^3 s^{-1}$)		Photoperiod (h)	
	SEP–FEB	MAR–AUG	SEP–FEB	MAR–AUG	SEP–FEB	MAR–AUG
Variable range	6.7–15.1	7.9–16.5	0.19–24.62	0.23–16.37	8.99–13.24	11.16–15.38
Movement range	7.4–14.8	9.2–14.5	0.20–19.09	0.23–7.73	8.99–12.86	11.26–15.38

b) Spearman correlations between variables

	Water temperature (T)	Variation in water temperature (ΔT)	River flow (Q)	Variation in river flow (ΔQ)	Photoperiod (P)
Water temperature (T)	1	$\rho = 0.0818$ p-Value $= 0.2345$	$\rho = -0.6738$ p-Value < 0.0001	$\rho = 0.1020$ p-Value $= 0.1377$	$\rho = 0.5692$ p-Value < 0.0001
Variation in water temperature (ΔT)	$\rho = 0.0829$ p-Value $= 0.2073$	1	$\rho = -0.0037$ p-Value $= 0.9567$	$\rho = -0.3473$ p-Value < 0.0001	$\rho = -0.0012$ p-Value $= 0.9858$
River flow (Q)	$\rho = -0.6195$ p-Value < 0.0001	$\rho = 0.0085$ p-Value $= 0.8975$	1	$\rho = 0.0622$ p-Value $= 0.3667$	$\rho = -0.3941$ p-Value < 0.0001
Variation in river flow (ΔQ)	$\rho = 0.0816$ p-Value $= 0.2148$	$\rho = -0.0844$ p-Value $= 0.1990$	$\rho = 0.2438$ p-Value $= 0.0002$	1	$\rho = 0.0472$ p-Value $=0.4928$
Photoperiod (P)	$\rho = 0.6787$ p-Value < 0.0001	$\rho = -0.0158$ p-Value $= 0.8108$	$\rho = -0.4282$ p-Value < 0.0001	$\rho = 0.0230$ p-Value $= 0.7265$	1

configuration of the capture system, downstream migration occurred by the volitional drop of fish over the weir, and therefore, it was not possible to monitor. The number of captures in the fishway was also likely to correspond to high part of the migratory population of the river reach, as captures in the fishway depend on its attraction and passage efficiency, and also on the distance from the original point that fish start the migration (Bunt et al., 2012). Regarding the use by species, apart from a single salmon (female, 810 mm FL, captured on November 2010), potamodromous brown trout was the only species found using the fishway. In this sense, due to the high number of captured trout and their FL range, Mugairi fishway could be considered non-selective by size. Moreover, the found relation between the population in the main stream Bidasoa River (sampled in summer) and the number of trout in the Marin River (captured in autumn–winter) could mean that adult trout live in the Bidasoa River because offers the habitat conditions (water depth and flow velocity among others) within the trout preference range for life and development, and then they migrate upstream to this smaller tributary for searching adequate conditions to spawn during the reproductive season (cf. Armstrong et al. (2003) for a review about trout habitat requirements depending on life stages).

4.1. Past and present scenarios

Captures were concentrated in November and December, extending in some years from October to January. These movements were mainly performed by sex identified adults and with large FL. This time interval agrees with the spawning migration period in the Iberian Peninsula (Doadrio, 2002; García-Vega et al., 2017), although in more southern populations spawning can extend until April (Gortázar et al., 2007; Larios-López et al., 2015).

Migrant female proportion was greater than male proportion, which differs with the observed in the mainstream Bidasoa River and some potamodromous populations of the center of the Iberian Peninsula (Duero and Tajo Basins) where both proportions were found to be similar (Almodóvar et al., 2006; Nicola and Almodóvar, 2002). Nevertheless, it is consistent with the values for anadromous Atlantic populations of the north of the Iberian Peninsula (2–3 females per male), where females are more likely to become anadromous, whereas males tend to stay in the river (Caballero et al., 2018, 2012). So, similary, it is possible that, in short Atlantic rivers as Bidasoa, females move from tributaries to the main stream for improving their growth while males stay in the tributaries becoming more resident.

In addition, our results showed that males migrated slightly earlier than females and larger individuals earlier than shorter ones. This agrees with the fact that, in salmonids, males usually enter the spawning grounds before females, where large males display agonistic behavior to establish and maintain dominance (Esteve, 2017; Jonsson and Jonsson, 2011).

Outside of the spawning period, less movements were observed. This movements were mainly performed by sex unidentified trout with shorter FL, which were associated with juvenile stages, and seem to be related to their ecological requirements as thermoregulatory behavior, feeding or exploration (Lucas et al., 2001). The existence of movements outside the spawning migration period demonstrates the

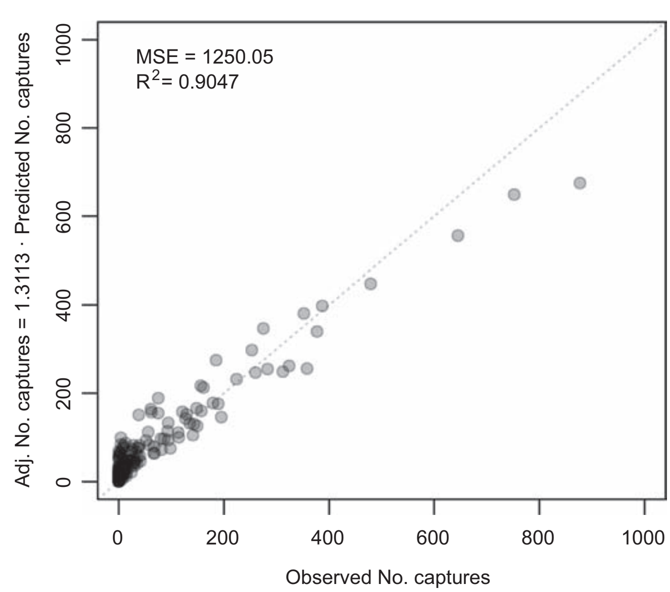

Fig. 8. Observed against predicted counts for RF regression after linear bias adjustment. RF regression was only applied for the data of the period autumn–winter (from September to February) with n = 11,023 captured trout.

importance of guaranteeing a correct performance of fishways throughout the whole year (García-Vega et al., 2017).

Regarding the developed RF model for predicting the timing and quantification of the migration, it showed a very good performance in the prediction of the migration timing. However, although it also showed a good performance in the prediction of number of captures ($R^2 = 0.91$), some deviations were detected. This can be explained by the existence of other variables not considered in the model, for example, the relation with the population in the Bidasoa River, i.e., captures depend not only on the environmental conditions but also in the available stock in the river. This available stock is the reflect of environmental conditions of previous years, that, in turn, conditions the spawning, larval development, juvenile survival and recruitment of the trout population (Caudill et al., 2013; Flitcroft et al., 2016; Moraes and Deverat, 2016; Young, 1999).

The decrease in photoperiod and water temperature, as well as the increase in river flow were identified as predictable variables in the model. Fish use the photoperiod as indicator of the season because it intervenes in the hormonal regulation during fish maturation (Jonsson, 1991). However, its importance in the model was lower than other variables. This can be explained because the day length is the same on each specific day every year. Thus, it had an important effect to identify the season when spawning migration is more likely to occur, but inter-annual variation in time of migration were induced by other

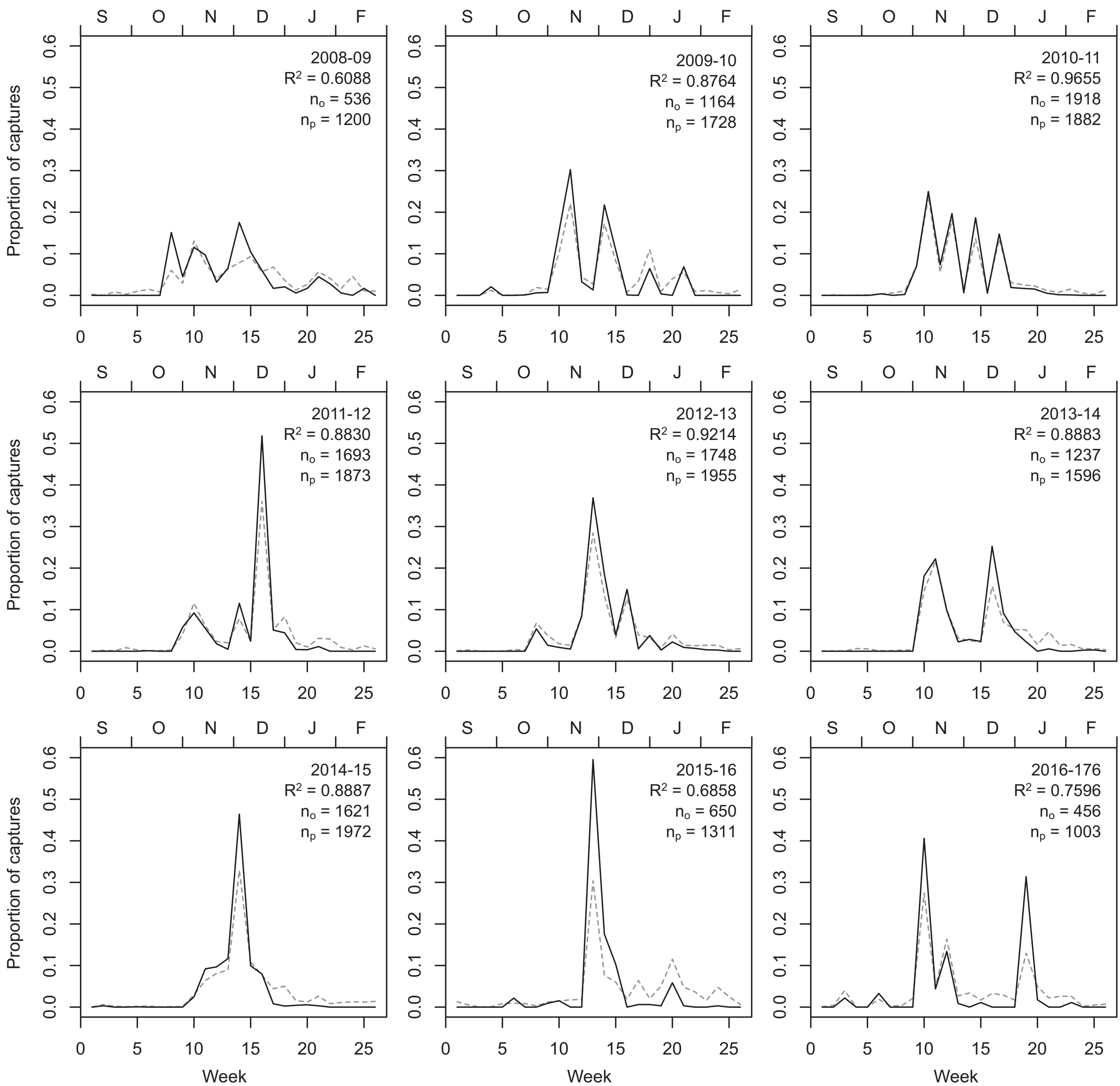

Fig. 9. Evaluation of the migration timing: observed (black solid line) and predicted (gray dashed line) proportion of captures for the period September–February (R^2 = coefficient of determination of the adjustment between the proportion of observed and predicted captures; n_o = observed number of captures; n_p = predicted number of captures).

environmental variables. These variables may shift from one river to other or even within the same river (Benitez and Ovidio, 2017). The decrease in water temperature was identified as the most important cue in the Marin River. This variable influences internal physiological processes for gonadal development (Lahnsteiner and Leitner, 2013). However, these changes in water temperature must be inside of a specific range. Lower temperature than this favorable range can retard maturation in fishes (due to its influence on the endocrine function, lipid accumulation and, in general, in the metabolism), whereas higher temperatures can have deleterious effects (gametogenesis inhibition and gamete viability) (Jonsson and Jonsson, 2011). In combination with the decrease in photoperiod and water temperature, river flow showed influence on trout upstream movements. Usually, the increase in water flow is considered a stimulant factor (Clapp et al., 1990; García-Vega et al., 2017) and a facilitator for overcoming obstacles (Ovidio and Philippart, 2002). Our results showed that discrepancies on the onset of migration between years were mainly due to the timing of the flow rate increase.

4.2. Future scenarios

The effects of alterations on river flow and thermal regimens, as climate change or river regulation, particularly affect to the Salmonidae family, which comprises oxygen demanding species that require cold and clean water (Jonsson and Jonsson, 2011), and specially to the brown trout, as it has lower tolerance to high temperatures than other salmonid species (Elliott and Elliott, 2010) and needs relatively high flows during its upstream migrations (Cragg-Hine, 1985) and moderate flows in post-spawning periods (Nicola and Almodóvar, 2002). The effects of climate change are especially relevant in its southern distribution area, where higher temperatures and longer and more often droughts are expected (Hermoso and Clavero, 2011).

RF model showed that water warming in SEM region as consequence of climate change (scenario 1) may suppose mainly a delay on the median spawning migration date. In addition, as the model maintained invariant the rest of parameters, a higher number of migrants was expected. However, this increment does not mean a higher reproductive success and it is expected that climate change will suppose a decline of brown trout population, overall in its southern distribution range (Almodóvar et al., 2012), due to its influence on physiological, behavioral and ecological traits. Physiologically, water warming reduces the gamete quality, and consequently the fertility. Lahnsteiner and Leitner (2013) analyzed the quality of gametes of brown trout under different water temperatures, obtaining fertility rates higher than 65% for males and 80% for females in the when 7.4 ± 4.6 °C, with negative effects on the reproductive potential when temperature surpassed 12 °C. In terms of behavior, water warming may produce a mislead among the cues that affect the timing of the spawning migration, leading a delay on the reproduction. In addition, with warmer climate, a shorter incubation period and earlier emergence time are expected (Jonsson and Jonsson, 2009). Moreover, a mismatch among offspring hatch and their ecological requirements, as food availability (Dingle and Drake, 2007; McLaughlin et al., 2013) or the flow reduction necessary to fish initial development (Nicola et al., 2009) could occur. Finally, the different co-stressors of the water warming, could affect to the ecology of the brown trout, with loss of suitable thermal habitat as the most important impact affecting its populations (Almodóvar et al., 2012).

When a scenario of constant low flow was modelled (scenario 2 of water regulation), in addition of a delay in the median migrate date, it results on a progressive migration, with lower expected number of migrants. This was evident when a mixed scenario of constant low flow and water warming was modelled (scenario 3). Results of the past models showed that the migration occurred in pulses triggered by

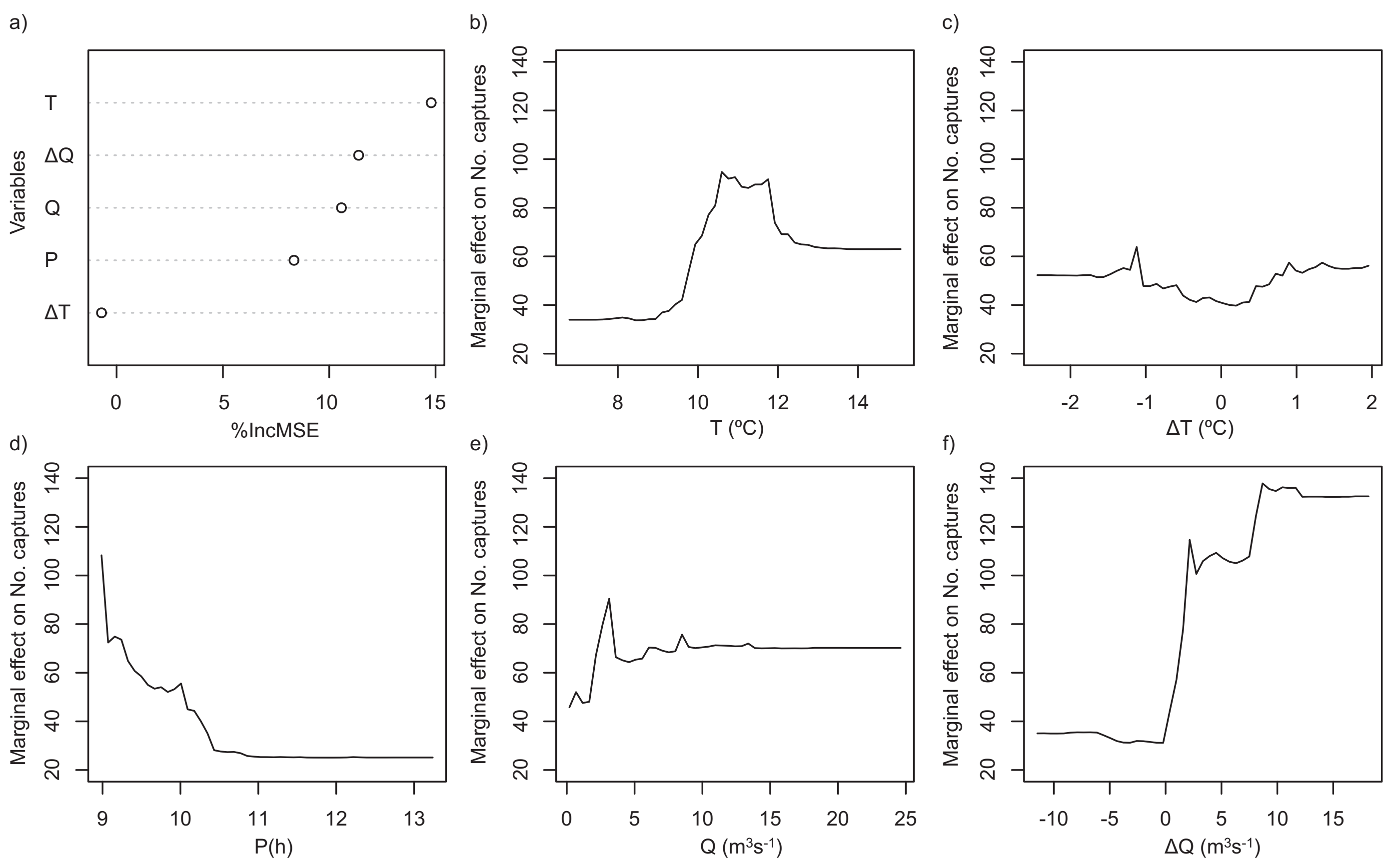

Fig. 10. a) Variable importance of the RF model in terms of increase in mean squared error (IncMSE); b) to f) partial dependence plots.

the local increase in flow rate. So, the anthropogenic alteration in flow regimen may produce the loss of this signal for upstream migration, which enhances the need of an optimal design and delivery of environmental flows. In addition, low flows can affect to the habitat availability, connectivity of habitats, obstacle ascent and increase the vulnerability to predation (Jonsson and Jonsson, 2009). On the other hand, flow reduction in post-spawning periods is essential to promote the survival of early life stages and recruitment (Nicola and Almodóvar, 2002).

5. Conclusions

This study showed that climate change and flow regulation may endanger potamodromous brown trout populations by directly affecting the reproductive migration timing. For past and present migrations, our study showed that a wide size range of potamodromous brown trout performs upstream movements throughout the year, more concentrated during spawning season, but also outside of the reproductive window, with a combination of variables as stimulus for the migration.

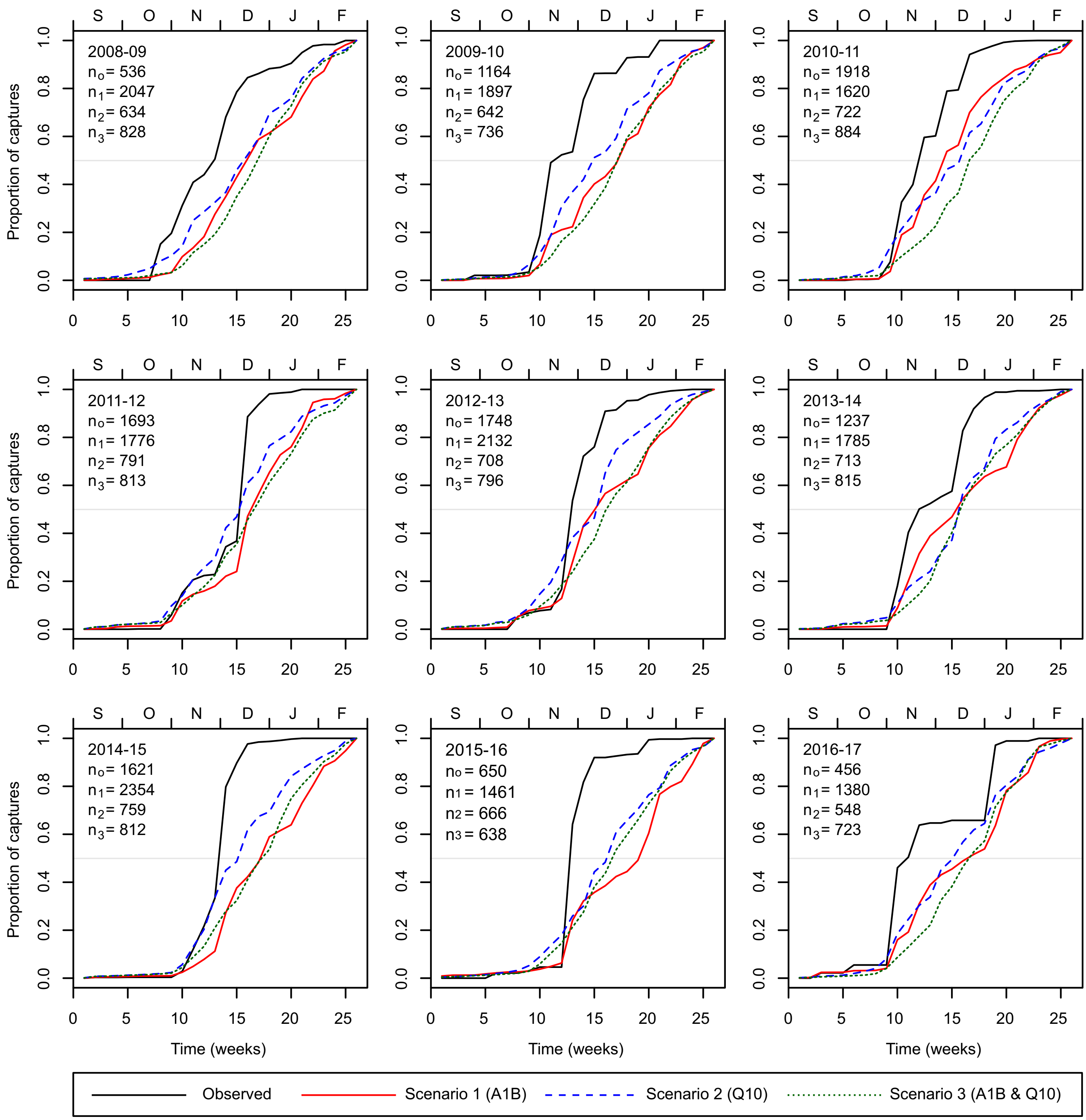

Fig. 11. Cumulative proportions of captures against time for past and future modelled scenarios for the period September–February: (o) observed past scenario; (1) scenario of water temperature increase (same increase as air temperature of IPCC A1B scenario); (2) scenario of water regulation (constant flow of 10% of the mean annual flow); and (3) combination of the scenarios 1 and 2.

The knowledge about migration patterns and the monitoring of fish populations is essential to assess the effect of human impacts (e.g. alterations of river flow and thermal regimens, overfishing, etc.) and in the management and decision making (optimal delivery of environmental flows, correct fishway design and operation, adequate scheduling of river restoration activities or fishing periods and quotas). In addition, modelling large time series can give us information about reach cues of the overall effect of changes in the parameters involved in the migration and, thus, prepare compensation measures and actions for possible impacts.

Acknowledgments

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Appendix A. Auxiliary tables

Table A.1
Characteristics of the captured trout by year and results of comparison tests (n = number of captured trout; FL = fork length; SD = standard deviation, H_0 = null hypothesis of the test).

Variable	2008–09	2009–10	2010–11	2011–12	2012–13	2013–14	2014–15	2015–16	2016–17[a]	Total
Total n	595	1192	1953	1693	1769	1263	1653	650	460	11,228
n male	154 (25.9%)	493 (41.4%)	748 (38.3%)	624 (36.9%)	667 (37.7%)	502 (39.7%)	654 (39.6%)	304 (46.8%)	203 (44.1%)	4349 (38.7%)
n female	388 (65.2%)	676 (56.7%)	1195 (61.2%)	1043 (61.6%)	1102 (62.3%)	749 (59.3%)	964 (58.3%)	345 (53.1%)	254 (55.2%)	6716 (59.8%)
n sex unidentified	53 (8.9%)	23 (1.9%)	10 (0.5%)	26 (1.5%)	0	12 (1%)	35 (2.1%)	1 (0.1%)	3 (0.7%)	163 (1.5%)
Sex rate (female:male)	2.5:1	1.4:1	1.6:1	1.7:1	1.7:1	1.5:1	1.5:1	1.1:1	1.3:1	1.5:1
p-Value binomial test (H_0: n male = n female)	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001	0.1163	0.0192	<0.0001
n adult	585 (94.5%)	1116 (95.6%)	1909 (97.8%)	1629 (96.2%)	1712 (96.8%)	1223 (96.4%)	1593 (96.7%)	634 (96.1%)	427 (94.9%)	10,828 (96.4%)
n juvenile	34 (5.5%)	52 (4.4%)	44 (2.2%)	64 (3.8%)	57 (3.2%)	45 (3.6%)	55 (3.3%)	26 (3.9%)	23 (5.1%)	400 (3.6%)
FL range (mm) global	130–570	125–620	135–580	118–650	120–640	90–630	40–550	150–450	110–460	40–650
Mean FL ± SD (mm) global	287.7 ± 56.4	291.7 ± 63.0	292.4 ± 53.3	318.9 ± 82.0	302.1 ± 75.7	303.3 ± 67.7	280.7 ± 54.5	290.9 ± 51.2	285.8 ± 57.4	296.8 ± 66.1
Median FL (mm) global	290	290	290	300	290	300	280	290	290	290
FL range (mm) male	168–535	125–620	150–580	140–650	120–640	140–600	115–530	160–450	110–460	110–650
Mean FL ± SD (mm) male	303.6 ± 63.6	296.6 ± 75.3	305.1 ± 57.8	341.9 ± 97.4	310.0 ± 82.6	307.6 ± 72.5	289.5 ± 56.6	302.6 ± 52.0	296.4 ± 65.0	307.5 ± 74.1
Median FL (mm) male	310	300	300	330	300	300	290	300	300	300
FL range (mm) female	170–570	150–530	135–530	118–630	130–630	150–630	160–550	150–450	140–440	118–630
Mean FL ± SD (mm) female	291.6 ± 45.8	290.7 ± 51.2	285.248.2 ±	309.0 ± 65.2	297.2 ± 70.9	302.9 ± 61.7	278.9 ± 48.0	280.7 ± 48.4	279.3 ± 43.2	292.4 ± 57.7
Median FL (mm) female	290	280	280	300	290	290	270	280	280	280
FL range (mm) sex unidentified	130–310	150–260	140–280	140–190	–	90–180	40–270	–	110–140	40–310
Mean FL ± SD (mm) sex unidentified	212.3 ± 46.3	216.0 ± 32.4	203.5 ± 37.9	167.3 ± 15.4	–	150.8 ± 27.5	166.7 ± 50.6	300.0±	126.7 ± 15.3	189.8 ± 47.6
Median FL (mm) sex unidentified	220	220	195	170	–	160	180	300	130	190
p-Value MW test (H_0: median FL male = FL female)	0.0054	0.0994	<0.0001	<0.0001	0.0001	0.0762	<0.0001	<0.0001	<0.0001	<0.0001
p-Value MW test (H_0: FL sex identified = FL sex unidentified)	<0.0001	<0.0001	<0.0001	<0.0001	–	<0.0001	<0.0001	0.8039	0.0032	<0.0001

[a] Incomplete year of fishway monitoring which was ended at March.

Table A.2
Pairwise comparison for differences in FL among years. The upper number is Dunn's pairwise *z* test statistic and the lower number the *p*-value associated with the test.

	2008–09	2009–10	2010–11	2011–12	2012–13	2013–14	2014–15	2015–16
2009–10	−0.2495 1.0000							
2010–11	−0.6191 1.0000	−0.4478 1.0000						
2011–12	−7.7696 <0.0001	−9.4621 <0.0001	−10.2788 <0.0001					

(continued on next page)

Table A.2 (*continued*)

	2008–09	2009–10	2010–11	2011–12	2012–13	2013–14	2014–15	2015–16
2012–13	−2.0428	−2.2492	−2.0665	8.0436				
	0.7393	0.4410	0.6980	0.0000				
2013–14	−3.8764	−4.4629	−4.5355	4.7750	−2.6042			
	0.0019	0.0001	0.0001	<0.0001	0.1658			
2014–15	3.8143	5.1287	6.3242	15.9826	8.1607	10.0368		
	0.0025	<0.0001	<0.0001	<0.0001	<0.0001	<0.0001		
2015–16	−1.1290	−1.0568	−0.7744	6.6367	0.7142	2.6660	−5.3224	
	1.0000	1.0000	1.0000	0.0000	1.0000	0.1382	<0.0001	
2016–17	0.2095	0.4651	0.8103	7.2898	2.0982	3.7782	−3.2126	1.2647
	1.0000	1.0000	1.0000	0.0000	0.6459	0.0028	0.0237	1.0000

Table A.3
Number of captures by month and year. Summaries for autumn–winter (from September to February) and spring–summer (from March to April) periods are shown.

	2008–09	2009–10	2010–11	2011–12	2012–13	2013–14	2014–15	2015–16	2016–17	Sum	Mean	SD
SEP	0	24	0	0	0	0	5	0	10	39 (0.3%)	4	8
OCT	105	16	11	2	105	0	1	20	15	275 (2.4%)	31	43
NOV	167	585	1139	383	832	648	977	449	270	5450 (48.5%)	606	327
DEC	190	420	692	1201	662	512	613	137	5	4432 (39.5%)	492	362
JAN	62	119	74	107	138	70	25	42	151	788 (7.0%)	88	43
FEB	12	0	2	0	11	7	0	2	5	39 (0.3%)	4	5
MAR	2	0	0	0	0	3	0	0	4	9 (0.1%)	1	2
APR	33	0	0	0	0	0	16	0	–	49 (0.4%)	6	12
MAY	15	8	5	0	21	6	16	0	–	71 (0.6%)	9	8
JUN	9	14	0	0	0	15	0	0	–	38 (0.3%)	5	7
JUL	0	6	22	0	0	0	0	0	–	28 (0.2%)	4	8
AUG	0	0	8	0	0	2	0	0	–	10 (0.1%)	1	3
Sum	595	1192	1953	1693	1769	1263	1653	650	460	11,228	1248	563
Sum SEP–FEB	536 (90.1%)	1164 (97.7%)	1918 (98.2%)	1693 (100%)	1748 (98.8%)	1237 (97.9%)	1621 (98.1%)	650 (100%)	456 (99.1%)	11,023 (98.2%)	1225	563
Sum MAR–AUG	59 (9.9%)	28 (2.3%)	35 (1.8%)	0 (0%)	21 (1.2%)	26 (2.1%)	32 (1.9%)	0 (0%)	4 (0.9%)	205 (1.8%)	23	19

Table A.4
Pairwise comparison for differences in number of captures by month. The upper number is Dunn's pairwise z test statistic and the lower number the p-value associated with the test.

	JAN	FEB	MAR	APR	MAY	JUN	JUL	AGO	SEP	OCT	NOV
FEB	2.8040										
	0.1666										
MAR	3.7576	0.9537									
	0.0057	1.0000									
APR	3.3538	0.6336	−0.2916								
	0.0263	1.0000	1.0000								
MAY	2.0950	−0.6252	−1.5504	−1.2233							
	1.0000	1.0000	1.0000	1.0000							
JUN	3.1492	0.4290	−0.4962	−0.1988	1.0245						
	0.0540	1.0000	1.0000	1.0000	1.0000						
JUL	3.5095	0.7893	−0.1359	0.1513	1.3746	0.3501					
	0.0148	1.0000	1.0000	1.0000	1.0000	1.0000					
AGO	3.7319	1.0117	0.0865	0.3674	1.5908	0.5663	0.2161				
	0.0063	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000				
SEP	3.4031	0.5991	−0.3546	−0.0524	1.2064	0.1522	−0.2081	−0.4305			
	0.0220	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000			
OCT	1.5528	−1.2512	−2.2049	−1.8474	−0.5886	−1.6428	−2.0031	−2.2255	−1.8503		
	1.0000	1.0000	0.9063	1.0000	1.0000	1.0000	1.0000	0.8595	1.0000		
NOV	−1.0433	−3.8473	−4.8010	−4.3660	−3.1072	−4.1614	−4.5217	−4.7441	−4.4464	−2.5961	
	1.0000	0.0039	0.0001	0.0004	0.0623	0.0010	0.0002	0.0001	0.0003	0.3112	
DEC	−0.6399	−3.4438	−4.3975	−3.9746	−2.7158	−3.7700	−4.1303	−4.3527	−4.0429	−2.1926	0.4035
	1.0000	0.0189	0.0004	0.0023	0.2182	0.0054	0.0012	0.0004	0.0017	0.9350	1.0000

Table A.5
Comparison tests for differences in the environmental variables among years: a) KW test (photoperiod was excluded as it is the same all years). b) Pairwise comparison for differences in mean weekly flow among years. The upper number is Dunn's pairwise z test statistic and the lower number the p-value associated with the test. Values above the diagonal correspond to the spring–summer (MAR–AUG) period and below the diagonal to the autumn–winter (SEP–FEB) period.

a) KW test

Variable	Whole year (SEP–AUG)	Autumn–winter (SEP–FEB)	Spring–summer (MAR–AUG)
Water temperature	Chi-squared = 1.6090	Chi-squared = 5.5714	Chi-squared = 1.1217
	p-Value = 0.9783	p-Value = 0.6951	p-Value = 0.9926
River flow	Chi-squared = 37.1700	Chi-squared = 17.6000	Chi-squared = 41.7430
	p-Value < 0.0001	p-Value = 0.0244	p-Value < 0.0001

b) Dunn test for river flow variable

	2008–09	2009–10	2010–11	2011–12	2012–13	2013–14	2014–15	2015–16
2008–09	–	0.6876	1.6733	−0.1306	−3.1810	−2.8289	−1.9885	−1.0080
		1.0000	1.0000	1.0000	0.0205	0.0654	0.6545	1.0000
2009–10	1.7446	–	0.9952	−0.8194	−3.8985	−3.5431	−2.6948	−1.7118
	1.0000		1.0000	1.0000	0.0014	0.0055	0.0986	1.0000
2010–11	3.5280	1.8006	–	−1.8052	−4.8842	−4.5288	−3.6806	−2.7070
	0.0075	1.0000		0.9947	0.0000	0.0001	0.0033	0.0951
2011–12	2.5819	0.8373	−0.9715	–	−3.0504	−2.6983	−1.8579	−0.8761
	0.1768	1.0000	1.0000		0.0320	0.0976	0.8845	1.0000
2012–13	1.3290	−0.4156	−2.2121	−1.2529	–	−0.8761	1.1924	2.2029
	1.0000	1.0000	0.4853	1.0000		1.0000	1.0000	0.3864
2013–14	1.5430	−0.2016	−2.0002	−1.0389	0.2140	–	0.8404	1.8475
	1.0000	1.0000	0.8186	1.0000	1.0000		1.0000	0.9054
2014–15	0.9011	−0.8435	−2.6358	−1.6808	−0.4279	−0.6419	–	0.9993
	1.0000	1.0000	0.1511	1.0000	1.0000	1.0000		1.0000
2015–16	1.9030	0.1584	−1.6437	−0.6789	0.5740	0.3600	1.0019	–
	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	
2016–17	2.7218	0.9772	−0.8330	0.1399	1.3928	1.1788	1.8207	0.8188
	0.1169	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000	1.0000

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